移位因子、遺傳變異與作物改良

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引 言

作物族群內遺傳變異的大小，一直是育種家著重而感興趣的，因為有了遺傳變異，選種才有效，過去50年的研究結果發現移位因子(transposable elements)是一個引起遺傳變異的重要原因，而在高等植物中以玉米內的移位因子(TE)被研究的最多，也最詳盡，故現舉玉米為例來說明TE、遺傳變異與作物改良三者間可能的關聯。

玉米的移位因子

一個移位系統包含了一個自主性因子或稱調節因子(autonomous element 或 regulatory element)，及對自主性因子有反應的非自主性因子或稱接受因子(nonautonomous element 或 receptor)，它們之間的交感作用使得植物組織如葉片、種子外表產生斑點(spots)、條紋(stripe)等斑雜(variegation)的現象。

自主性因子與非自主性因子間若有專一性(specific)的交感作用，則它們就屬同一家族(family)，玉米的移位因子系統現今至少被發現有14個家族，如表1所列，其中有的接受因子沒有被賦予固定的名稱，為了要瞭解玉米移位因子在遺傳上的基本特性，現以 Dr. Peterson 實驗室所發現的 Uq 系統為例做一說明。

一、Uq 移位因子系統

這是一個新的 two-element controlling system，1967年 Sprague 和 Mckinney 在 Wheat Streak Mosaic Virus (WSMV) 感染的玉米中發現有籽粒表現出異常比例的斑雜，將此籽粒種植自交的後代交由 Peterson 做進一步的遺傳分析，而以 Ac538 為這種子的代號。(見Fig.1)，這是關於 Uq 這個系統研究的開始。至於為何命名為 Uq system，乃是因為在這系統中的 controlling element 可以在許多 inbred lines 及 testers 中被發現，故取其"到處存在" Ubiquitous(Uq) 之意，而稱之為 Uq-system。下面我們將討論如何由遺傳分析的方法去探討 Uq ，及 Uq 在玉米不同族群中的分佈。

(一)確定Ac538的基因型

使用有斑雜的 Ac538 和不同的隱性同型結合之材料做相互雜交，這些材料分別為 a^2/a^2，c/c 或者 r/r 的基因型，雜交的結果發現只產生有顏色的籽粒。這表示在子代當中 A^2、C或者R

基因座並非同質結合。把它拿來跟以 Ac538 和 a-o testers 雜交的結果做比對，由於後者雜交結果會引起斑雜籽粒的發生。因此可確定 Ac538 的基因型是 A^2/A^2、C/C、R/R ，而斑雜的控制

Table 1 The transposable element systems in maize listed as Regulatory-receptor combinations. Homologous elements are listed in parentheses (Peterson, in press). The receptor alleles (MERL) used in the BSSS series of crosses are identified with an asterisk*;--indicates no identifiable named receptor.

	Regulatory	Receptor element	Receptor allele	References
1	Dt	Dt	a(rDt)*	Rhoades (1936)
2	Ac (Mp)	Ds	CDs*	McClintock (1947); Brink and Nilan (1952)
3	En (Spm)	I	a(mr)*	Peterson (1953); McClintock (1954)
4	Fcu (Spf)	rcu	rcu*	Gonella and Peterson (1977)
5	Uq	ruq	a-ruq* c-ruq*	Friedemann and Peterson (1982) Oberthur and Peterson (1984)
6	Bg	rBg	o2m(r)*	Salamini (1981)
7	Mrh	rMrh	a(rMch)*	Rhoades and Dempsey (1982)
8	Mut	rMut		Rhoades and Dempsey (1982)
9	c2-m3	—		Peterson (1984)
10	Cy	rcy		Schnable and Peterson (1984)
11	Mul	—		Robertson (1978)
12	M-st	I-R		Kermicle (1984)
13	BSl	—		Johns *et al.* (1985)
14	Tz	—		Dellaporta *et al.* (1984)

(Peterson, P.A. 1986)

基因是在 A 基因座。不過在這個 Ac538 與 a-o tester 的雜交結果當中，除了斑雜籽粒以外，尚有二種原先不被期望的籽粒性狀，有顏色以及無 a-m/a-m × a-o/a-o → a-m/a-o (variega-

ted expected) <cross 1> 色籽粒。暫且推測可能是由於可以產生斑雜的 a-m 突變成 A 產生有色籽粒，或者由於控制斑雜的因子消失使 a-m 突變成 a 所以有無色籽粒產生。

(二)Regulatory element (Uq)，Receptor element (a-ruq)

爲了確定斑雜發生的原因，所以取前述 cross 1 所得到的斑雜籽粒種植，和 a-o sh2 做雜交 (cross 2)，產生不同比例的後代表型 (table 2)。

a-m Sh2/a-o sh2 × a-o sh2/a-o sh2 (from cross 1) <cross 2>

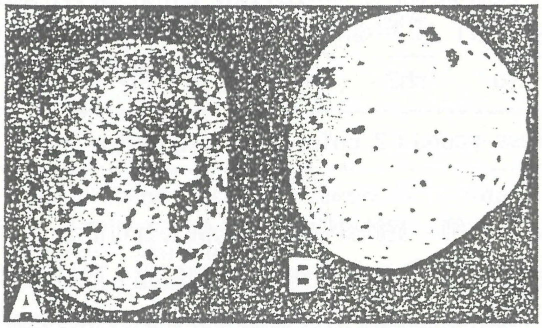


Fig.1 Patterns of spotting of kernels from Ac 538. Kernel A illustrates a coarse-high pattern of spotting. Kernel B illustrates a fine-low pattern of spotting (Friedemann and Peterson 1982).

Table 2 Phenotypic frequencies from the cross a-m^2 Sh2/a-o sh2 × a-o sh2/a-o sh2 (Friedemann & Peterson 1982)

Progeny ear (1977)		Kernel number(%)				χ^{2b}
		Round		Shrunken colorless	Total	
		Spotted	Colorless			
1.	2048-1	119 (39.7)	24 (8.0)	157 (52.3)	300	60.8**
2.	2048-2	75 (36.6)	33 (16.1)	97 (47.3)	205	17.8**
3.	2048-3	71 (26.0)	72 (26.4)^c	130 (47.6)	273	0.6ns^2
4.	2048-4t	80 (36.9)	16 (7.4)	121 (55.8)	217	40.6**
5.	2048-5	65 (41.9)	14 (9.0)	76 (49.0)	155	33.6**

a a-m refers to the a allele expressing mutability observed in Ac538 (Fig.2)

b χ^2 value for a segregation of 1 spotted-round: 1 colorless-round: 2 colorless-shrunken. *P($^b\chi^2$>5.99)<0.05, **P($^b\chi^2$>9.21)<0.01 (see cross 3)

c Source of colorless-round and colorless-shrunken kernels in crosses giving progeny listed in Table 2

d ns=χ^2 not significant at 0.05 level

** Significant at 0.01 level; t=tiller

如按照上述假設，則在 table 2 中理應只有斑雜圓形(a-m Sh2/a-o sh2)：無色皺縮(a-osh2/a-osh2)=1：1。然而在table 2 中顯示尚有無色圓形的外表型存在，是以相信應該另外有一個控制因子(regulatory elements)，其運作獨立於 A 基因座。假設基因型如下：(Uq:regulatory element)

$$\frac{a\text{-}m}{a\text{-}o}\quad\frac{Sh2}{sh2}\quad\frac{Uq}{+}\quad\times\quad\frac{a\text{-}o}{a\text{-}o}\quad\frac{sh2}{sh2}\quad\frac{+}{+}$$ <cross 3A>

↓

$$\frac{a\text{-}m}{a\text{-}o}\quad\frac{Sh2}{sh2}\quad\frac{Uq}{+}\ :\ \frac{a\text{-}m}{a\text{-}o}\quad\frac{Sh2}{sh2}\quad\frac{+}{+}\ :\ \frac{a\text{-}o}{a\text{-}o}\ \frac{sh2}{sh2}\quad\frac{+}{+}\ \text{or}\ \frac{Uq}{+}$$

1 spotted round：1 colorless-round：2 colorless shrunken。

結果表 2 中只有 2048-3 符合這個比例。至於其它 4 個比例，有可能是 2 個以上的因子控制或者是這個因子很接近 A 基因座。爲了印證上述 cross 3A 的假設，取符合比例的 2048-3植株當中 colorless round 及 colorless-shrunken 籽粒種植，並且進行相互雜交 (cross 3B)。在這裡，可以把由 Uq 在 A 基因座引起的突變基因稱作 a-ruq，這是這二因子控制系統中的 receptor element。

$$\frac{a\text{-}ruq}{a\text{-}o}\quad\frac{Sh2}{sh2}\quad\frac{+}{+}\quad\times\quad\frac{a\text{-}o}{a\text{-}o}\quad\frac{sh2}{sh2}\quad\frac{Uq}{+}\quad\text{or}\quad\frac{+}{+}$$ <cross 3B>

結果記錄在表 3，其中 line 4,8,9,11 符合 1:1:2 而 line 1,2,3,5,7,10，符合沒有 Uq 因子時 1 colorless round：1 colorless shrunken 的比例。不過 line 6 以及 12 的比例卻不相同。爲探討上述不合比例的原因，於是取 line 12 (1426-12) 的 colorless round 籽粒和colorless-shrunken。籽粒種植雜交 (cross 4) 結果顯示在表 4。

$$\frac{a\text{-}ruq}{a\text{-}o}\quad\frac{Sh2}{sh2}\quad\frac{+}{+}\quad\times\quad\frac{a\text{-}o}{a\text{-}o}\quad\frac{sh2}{sh2}\quad\frac{Uq}{+}\quad\text{or}\quad\frac{+}{+}$$ <cross 4>

原本預期應會只有如 cross 3 中progeny爲 1:1:2 (line 2,4,5,7) 或者 1:1 的表型出現(line 1,3,8) 結果竟然還有 1 spotted round：1 colorless shrunken 的表型比出現，造成這種結果的可能原因是兩親均帶有 Uq，但是有 Uq 的 a-ruq Sh2，不可能被選爲 colorless round 因其應爲 spotted ，唯一的解釋可能是 a-ruq 會改變成對 Uq 沒有反應的基因座，因此被以爲是無色圓形籽粒，然而它也可能在下個世代中又恢復原狀。最後我們再取1214-5 及 1214-14兩個 line 的 colorless round 籽粒分別做兩種雜交，結果列在表 5。

由 line 1-4 結果有 spotted 的情形看來，是由於 tester 提供了 Uq 故使 1214-5 所帶之 a-ruq 因 uq 之作用而表現spotted。而line 5-7 結果無spotted 可證實1214-5不帶有 Uq，

line 8-9 無 spotted，表示 1214-14 的 a-ruq 可能對 Uq 沒有反應，而 line 12 中由 1214-14 與 a-ruq 雜交，由於有外來的 a-ruq ，則可表現出 spotted ，更能印證了先前所提出的在 colorless round 的親本中含有對 Uq 沒有反應之改變過的 a-ruq。

其實，有時候斑雜的改變不見得一定與 Uq 有關 ，有可能只是 a-ruq 自發性的改變對 A locus 及性狀造成影響，例如 one-spot 籽粒的形成就是一個很好的例子 (3)，這是由於 a-ruq 的不穩定，而在發育過程中在糊粉層形成一個包含 1-24 個細胞的單一斑點，其發生並無 Uq 的介入 (Peterson & Friedemann 1983)。

Table 3 Phenotypic frequencies in crosses of colorless-round kernels by colorless-shrunken kernels or ear 2048-3 (Table 1, line 3) (Friedemann & Peterson 1982)

Progeny ear (1978)		Kernel number(%)				χ^{2a}	χ^{2b}
		Round		Shrunken colorless	Total		
		Spotted	Colorless				
1.	1426-1	0	323 (49.8)	325 (50.2)	648	0.006[c]ns[e]	
2.	1426-2	0	233 (53.1)	206 (46.9)	439	1.7ns	
3.	1426-3	0	114 (53.8)	98 (46.2)	212	1.2ns	
4.	1426-4	112 (23.8)	138 (29.3)	221 (46.9)	471		4.6ns
5.	1426-5	0	127 (54.5)	106 (45.5)	233	1.9ns	
6.	1426-6	59 (37.3)	21 (13.3)[d]	78 (49.4)	158		18.3**(deviant)
7.	1426-7	0	105 (51.5)	99 (48.5)	204	0.2ns	
8.	1426-8	48 (21.0)	68 (29.8)	112 (49.1)	228		3.6ns
9.	1426-9	98 (24.9)	106 (27.0)	189 (48.1)	393		0.9ns
10.	1426-10	0	103 (52.6)	93 (47.4)	196	0.5ns	
11.	1426-11	90 (23.2)	105 (27.1)	192 (49.6)	387		1.2ns
12.	1426-12	22 (14.0)	44 (35.0)[c]	80 (51.0)	157		13.9**(deviant)

a χ^2 value for a segregation of 1 colorless-round：1 colorless-shrunken. *P($^a\chi^2$>3.84)<0.05 **P($^a\chi^2$>6.63)<0.01

b χ^2 value for a segregation of 1 spotted-round：1 colorless-round：2 colorless-shrunken. *P($^b\chi^2$>5.99)<0.05, **P($^b\chi^2$>0.21)<0.01

c Source of colorless-round kernels in crosses with related colorless-shrunken kernels giving progeny listed in Table 3

d Source of colorless-round kernels in crosses with related colorless-shrunken kernels giving progeny listed in Table 8

e ns=χ^2 not significant at 0.05 level

(三) Uq 的劑量效應與性別的影響

我們用 2 個簡單的設計來看 Uq，a-ruq 以及性別對玉米籽粒外表型的影響。

1. a-ruq/a-ruq +/+ 和 a-ruq/a-ruq Uq/Uq 固定 progeny endosperm 中 a-ruq 的劑量均為 3 個。A. 以(甲)為♀親，B. 以(乙)為♀親。結果見(表 6)。可以發現在以 a-ruq/a-ruq，Uq/Uq

爲♀親的後代中幾乎全爲 coarse-high 的表型。而反之則爲 Fine-low 表型 。這可能是由於在前者子代胚乳中有 3 個 Uq，而後者只有一個 Uq 之故。這表示 Uq 存在有劑量效應。

Table 4 Phenotypic frequencies of progeny from colorless-round kernels of ear 1426-12 (Table 2, line 12) crossed by plants from related colorless-shrunken kernels (Friedemann & Peterson 1982)

Progeny ear (1979)	Kernel number(%)				χ^{2a}	χ^{2b}	χ^{2c}
	Round		Shrunken colorless	Total			
	Spotted	Colorless					
1. 1214-5	0	102 (51.5)[d]	96 (48.5)	198	0.2ns[e]		
2. 1214-6	48 (28.1)	42 (24.6)	81 (47.4)	171			0.9ns
3. 1214-7	0	132 (51.8)	123 (48.2)	255	0.3nx		
4. 1214-8	13 (26.0)	8 (16.0)	29 (58.0)	50			2.3ns
5. 1214-10	56 (22.2)	70 (27.0)	126 (50.0)	252			1.6ns
6. 1214-11	355 (53.1)	0	313 (46.9)	668		2.1ns	
7. 1214-12	53 (20.7)	62 (24.2)	141 (55.1)	256			3.3ns
8. 1214-14	0	167 (52.8)[d]	149 (47.2)	316	0.1ns		
9. 1214-15	275 (51.0)	0	264 (49.0)	539		0.1ns	

a χ^2 value for a segregation of 1 colorless-round：1 colorless-shrunken. *P($^a\chi^2$>3.84)<0.05, **P($^a\chi^2$>6.63)<0.01

b χ^2 value for a segregation of 1 spotted-round：1 colorless-shrunken. *P($^b\chi^2$>3.84)<0.05, **P($^b\chi^2$>6.63)<0.01

c χ^2 value for a segregation of 1 spotted-round ：1 colorless-round ：2 colorless-shrunken. *P($^a\chi^2$>5.99)<0.05, **P($^c\chi^2$>9.21)<0.01

d Source of colorless-round kernels in crosses giving progeny listed in Table 4

e ns=χ^2 not significant at 0.05 level

2. a-ruq/a-ruq，Uq/Uq 和 a-o/a-o，Uq/Uq 固定 Uq 的劑量，均爲 2 個。結果見表 7 。很清楚的從表 7 可以看到不論是以何者爲♀親其結果都是產生coarse-high，雖然兩種情形所得到的 a-ruq 數目並不相同，但卻一定可以有 Uq/Uq/Uq。是故均呈現 coarse-high 表型 。由此可知此劑量效應是由 Uq 所決定的，與 a-ruq 無關。

另外，我們還可以在一些實驗當中發現有特殊的潛伏性不活化 Uq(latent inactive Uq) 存在。當它在雜交用作♂親時，無法被探測出來，而只有在用作♀親時方可表現探知，這彷彿在♀♂中也有不同的劑量表現。(Peterson & Friedemann 1983)。

(四)靜默的 Uq 在胚乳發育中的表現

最近，在將野生植株經由組織培養後所得到的後代當中，發現有原來不活動的 Uq 被活化了，這再度印證了在從前的報告中曾指出的，由於環境變異的刺激可以使不活動的因子活化 (Fri-

Table 5 Presence or absence of spotted kernels from crosses involving colorless-round kernels of ears 1214-5 and 1214-14 (Table 3. lines 1 and 8. respectively) and an a-o/a-o line containing Uq and a-ruq-testers (Friedemann & Peterson 1982)

Progeny ear (1979)	Cross	Presence[a] of spotted progeny	Total Kernel number
1. 34/35-2	Colorless-round[b] × a-o/a-o, Uq/+	+	107
2. 34/35-4	Colorless-round[b] × a-o/a-o, Uq/+	+	182
3. 34/30-1	Colorless-round[b] × a-o/a-o, Uq/+	+	91
4. 34/30-3	Colorless-round[b] × a-o/a-o, Uq/+	+	66
5. 33/34-1	a-ruq/a-ruq, round +/+ × colorless-round[b]	-	51
6. 33/34-2	a-ruq/a-ruq, round +/+ × colorless-round[b]	-	40
7. 33/34-5	a-ruq/a-ruq, round +/+ × colorless-round[b]	-	64
8. 32-2/35-2	Colorless-round[c] × a-o/a-o, Uq/+	-	78
9. 32-3/30-3	Colorless-round[c] × a-o/a-o, Uq/+	-	42
10. 32-4/30-1	Colorless-round[c] × a-o/a-o, Uq/+	-	28
11. 34-3/32-2	a-ruq/a-ruq, round +/+ × colorless-round[c]	-	250
12. 34-4/32-1	a-ruq/a-ruq, round +/+ × colorless-round[c]	+	139
13. 33/32-3	a-ruq/a-ruq, round +/+ × colorless-round[c]	-	122

a += the presence of spotted kernels, indicating the simultaneous presence of both an a-ruq receptive allele and an Uq regulatory element. - = the absence of spotted kernels, indicating the absence of one or both a-ruq and Uq in the progeny genome
b Colorless-round selections from ear 1214-5 (Table 3, line 1)
c Colorless-round selections from ear 1214-14 (Table 3, line 8)

edemann & Peterson 1982, Pan & Peterson 1988, Peterson & Friedemann 1983)。Uq 存在很多的 inbred line 和 testers 中，也在 BSSS (Iowa Stiff Stalk Synthetic)玉米族群中發現，但是卻不能在由 BSSS 所育成的 inbred line 以及其它商業用的 inbred line 找到有活性的Uq。這可能是由於強大的淘汰斑雜籽粒，人爲的選種壓力所致。不過我們在前面曾提及即使在沒有具活性的 Uq 情況下，仍然以相當低的比例出現斑雜 (one-spot)。這是由於一種不會遺傳的 a-ruq 基因不穩定的關係。既然有這樣的情形，那麼是不是還有其它的因子，可以使得不具有活性Vq 因子的 inbred line 出現斑點呢？在底下這個對 4 個 inbred line 所做的試驗中可以發現另一種形態的表現與控制。

在一些由 standard a-ruq tester 與 inbred line 的雜交籽粒中常會發現一種特殊的斑塊(sector)性狀，這與我們原先所知道的由 r/r/R 所造成的 mottled 性狀很類似，因此我們將此種籽粒的植株與 a-ruq tester 做回交 (見 Fig.2)，並且取其有斑塊性狀的籽粒種植 (BC_1) ，有 25 棵長成，然後對 R-locus 做數次 test cross 之後 ，證明其爲 R/R 或者 r/R 的基因型

Table 6 Phenotypic frequencies from paired-plant reciprocal crosses of the genotypes a-ruq/a-ruq, +/+ and a-ruq/a-ruq, Uq/Uq (Friedemann & Peterson 1982)

Reciprocal crosses[a] (1980)	Kernel number				Total
	Colored	Colorless	Fine-low[b]	Coarse-high[c]	
1. A. 1027-1/1030-2	-	-	208	-	208
B. 1030-2/1027-1	1	-	-	252	253
2. A. 1027-3/1033-9	2	-	241	-	243
B. 1033-9/1027-2	1	-	-	182	183
3. A. 1028-1/1030-1	1	-	254	-	255
B. 1030-1/1028-1	-	-	-	202	202
4. A. 1028-6/1029-4	2	-	364	-	366
B. 1029-4/1028-6	5	-	1	250	256
5. A. 1028-7/1029-5	-	-	341	-	341
B. 1029-5/1028-7	-	-	2	192	194
6. A. 1028-11/1032-1	3	2	238	-	243
B. 1032-1/1028-11	-	-	-	110	110
7. A. 3110-9/3126-9	1	-	341	-	342
B. 3126-9/3110-9	5	-	-	358	363
8. A.[d] 3107-10/3127-6	3	-	372	-	375
B.[d] 3127-6/3107-10	-	-	-	338	338
9. A. 3107-11/3127-7	3	-	421	-	424
B. 3127-7/3107-11	2	-	-	224	226

a In each set of reciprocal crosses: line A is the cross a-ruq/a-ruq, +/+ ×a-ruq/a-ruq, Uq/Uq line B is the cross a-ruq/a-ruq Uq/Uq × a-ruq/a-ruq +/+

b One of two spotting patterns distinguished by a lower frequency of spots and a smaller size to the spots, represented in Fig.2

c One of two spotting patterns distinguished by a higher frequency of spots and a larger size to the spots, represented in Fig.2

d Source of the picture in Fig.3

，故不可能形成 mottled ，而是另有因素造成這種斑雜。這可能仍是 a-ruq 與 Uq 之間的作用，但是在 Fig 1 的雜交 BC_1 籽粒中可以得到 colored and mottled 與 colorless 籽粒的比例爲接近 1：1 (見 table 9) 這符合了 table 8 所示的 case 1，這表示了在此並無有活性的 Uq 因子存在。而可能是由一種類似 Uq 的活化作用所造成的。因此，另外將 BC_1 對 a-ruq tester 再做一次回交得到 BC_2 (table 10)，會發現即使這是 Uq 的活化所致的現象，這被活化了的 Uq 也不會遺傳至下一代，因爲在 BC_2 中並沒有發現正常比例的 Uq 典型斑雜 。另外我們還可以在

Table 7 Phenotypic frequencies from paired-plant reciprocal crosses of the genotypes a-ruq/a-ruq, Uq/Uq and a-o/a-o, Uq/Uq (Friedemann & Peterson 1982)

Reciprocal[a] crosses (1980)	Kernel number				Total
	Col-ored	Color-less	Fine-[b] low	Coarse-[c] high	
1. A.	1	-	-	371	372
B.	-	-	-	276	276
2. A.	2	-	1	340	343
B.	-	-	-	46	46
3. A.	1	-	-	281	282
B.	1	-	-	82	83
4. A.	-	-	-	376	376
B.	-	-	-	78	78

a In each set of reciprocal crosses: line A is the cross a-ruq/a-ruq, Uq/Uq × a-o/a-o, Uq/Uq line B is the cross a-o/a-o, Uq/Uq × a-ruq/a-ruq, Uq/Uq

b One of two spotting patterns distinguished by a lower frequency of spots and a smaller size to the spots, represented in Fig.2

c One of two spotting patterns distinguished by a higher frequency of spots and a larger size to the spots, represented in Fig.2

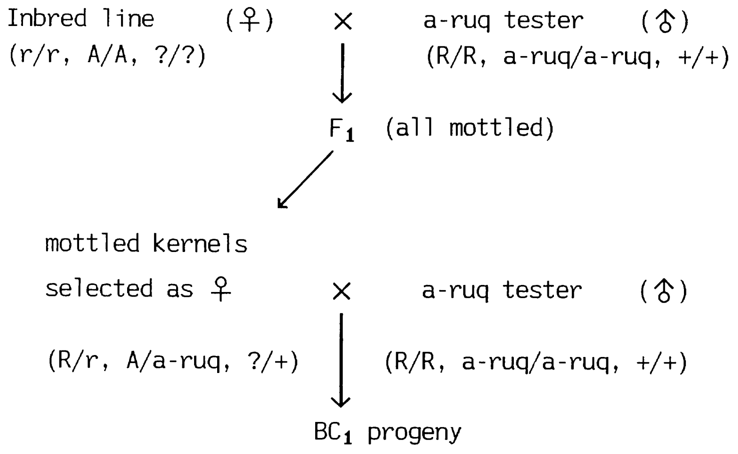


Figure 2 General crossing scheme to test the distribution of the Uq transposable element in maize inbred lines.The mottling is a characteristic feature of the r allele in the triploid endosperm when it is derived from the female in a cross yielding an R/r/r allelic condition while all the other color related genes are dominant. A question mark implies that the Uq content in each inbred line was not know at the time of test. a " + " indicates no active Uq is present. BC_1 is the first backcross generation. (Pan & Peterson 1988)

Table 8 Expected genotypic and phenotypic frequencies of BC_1 (Figure 1) progeny kernels under three possible cases[a] (Pan & Peterson 1988)

Genotype	Phenotype	Frequency[b]		
		Case I	Case Ⅱ	Case Ⅲ
A/a-ruq, +/+ or Uq/+	Colored and mottled	0.5	0.5	0.5
a-ruq/a-ruq, +/+	Colorless	0.5	0.25	0.125
a-ruq/a-ruq, +/Uq	Spotted	0	0.25	0.375

a All kernels carry at least one copy of R.
b Case I, when inbred line does not have any active Uq element; case Ⅱ, when inbred line has one active Uq element; and case Ⅲ, when inbred line has two nonallelic Uq elements.

Table 9 Phenotypic classification of the BC_1 progeny ears produced from the test-cross of the F_1 (inbred line X a-ruq tester) by a-ruq tester (Pan & Peterson 1988)

Inbred line	No.of ears	No.of kernels	Phenotypic classification (%)[a]					χ^{2b}
			Colored and mottled	Colorless				
				No-spot	Few-spotted	Sectored	Total	
B70	46	16,797	8,317	8,456	23	1	8,480	1.58(NS)
			(49.6)	(50.4)	(0.14)	(0.006)		
C103	63	24,734	12,265	12,380	86	3	12,469	1.68(NS)
			(49.5)	(50.1)	(0.35)	(0.01)		
C123	37	12,375	6,236	6,116	18	5	6,139	0.79(NS)
			(50.4)	(49.4)	(0.15)	(0.04)		
187-2	54	20,483	10,137	10,175	151	20	10,346	2.11(NS)
			(49.5)	(49.7)	(0.74)	(0.10)		
Grand total	200	74,389	36,955	37,127	278	29	37,434	

a Few-spotted indicates a colorless aleurone layer with 1 to 5 small color spots; sectored indicates a colorless aleurone layer with sector of color spots, size of sectors varies in different sectored kernels;
b A χ^2 value for case I in Table 1; NS=not significant at 0.05 level.

table 10 中看到只有在以 sectored BC_1 爲♀親的時候才會有較大的 mean frequency，至於其它的五組數據差別並不大，那也就是說在做這個回交時取的是 few-spot ，no-spot 籽粒做♀♂親或是以 sector 做爲♂親其所形成的斑塊籽粒並不會有差異，這暗示了這個 Uq 的活化可能是受某些與細胞質有關因素所影響，這在本實驗中可以從三個結果得到印證：

1.在由 sectored 籽粒在做爲♀親的時候所得到的 BC_2 具有較高比例的斑塊籽粒。

2.在 few-spot，no-spot 做爲♀♂以及 sectored 做爲♂親的 BC_2 中斑塊籽粒較少是因爲含有較少的促進因子的原故。

3.在將 standard a-ruq line 自交或近親交配的結果，常會有極低比例的 few-spot，而從來沒有斑塊性狀出現，但是當用它與其它的自交系或 tester 做雜交時才會有 sector (斑塊)的表現。

將此三點綜合，斑塊性狀的產生可能是在這些自交系或 tester 的基因組當中，可能是細胞質，具有促進靜默 Uq 活化的促進因子(enhancer)。

另外他們在此實驗中還分析這種斑塊的大小以及所在的位置，主要是以發生突變細胞的數目(斑塊大小)來推測 Uq 因子活化的時期，而利用其所在的位置來決定這個活化作用發生的位置。由 Fig 7 所得到的結果，我們可以看到多數的突變發生在極核受精後第 7 及第 13 次有絲分裂的時候，很少是在初期發生，這表示了這種使靜默 Uq 因子活化的促進作用是隨機發生的在細胞數目多時發生的機會就大，而在胚乳發育末期的突變，多半是不易被肉眼所察覺的。(Pan & peterson 1988)。

Table 10 Number and mean frequency of sectored kernels on colorless BC_2 progeny ears produced from the reciprocal backcrosses with a-ruq tester of plants grown from three types of BC_1 sib kernels (Pan & Peterson 1988)

BC_1 kernel type	No. of plants tested	Parental type[a]	No. of progeny ears	No. of colorless progeny kernels: Not sectored	Sectored	Spotted[c]	Total	Mean frequency of sectored kernels per individual BC_2 ear[b]
Sectored	25	M	15	3,382	16	0	3,398	0.00495±0.00088
		P	67	16,205	30	1	16,236	0.00167±0.00040
Few-spot	70	M	78	29,136	46	2	29,184	0.00152±0.00035
		P	107	32,137	62	0	32,199	0.00166±0.00032
No-spot	147	M	155	59,833	55	2	59,890	0.00102±0.00025
		P	102	27,084	23	1	27,108	0.00072±0.00035

a M. maternal; P. paternal.

b Estimated least squares mean frequency and standard error by a split plot analysis model of Cochran and Cox (1957).

c Confirmation of these events is in progress.

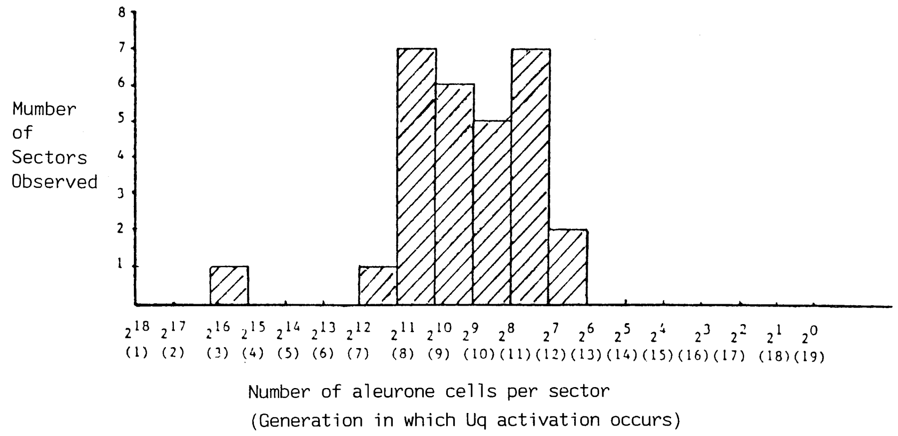


Figure 3: Histogram showing the activation of Uq leading to sectored kernels. This class occurs more frequently between 7th and 13th cell generation of endosperm growth. Even more frequently, activation events occur after generation 13. They, however, usually produce the few-spotted phenotype (Table 1) and, therefore, are not included here. This graph is based on a mature maize aleurone layer consisting of 160,000 cells (Stadler 1944). In order to produce an aleurone layer of this size, approximately 18 cycles of cell divisions are needed after fertilization. (Pan & Peterson 1988)

玉米 BSSS 族群與自交系

一、BSSS C0～C7 族群：

玉米 BSSS (Iowa Stiff Stalk Synthetic) C0 族群是由 16 個自交系相互交配而得。利用Ia13 爲檢定親，169 株的 C0 族群植株一面進行測交 (testcross 與檢定親交配)，一面進行自交，依測交結果選出最優良的 10 個 S_1 系統，再利用全互交方法產生 BSSS C1 的族群，依此程序分別產生 C2 至 C7 的族群，如圖 4 所示。

二、B13 族群：

因爲 Ia13 爲檢定親，故由 BSSS C7 起將族群改爲 BS13(S)C0 族群，依相同程序可得C2以後的族群。

三、自交系：

分別由不同 BSSS 輪迴族群中選育出來的 B14，B37，B84 ，每一個自交系自交約 6 個世代，亦請見圖 4。

四、BSSS 族群及自交系內移位因子的檢定：

利用下面圖示(圖 5)的步驟 (Peterson, 1986)，檢定 BSSS C0，C1，C3，C7 及 BS13(S) C2及 B14，B37，B73，B84 等自交系是否帶有移位因子。

檢定的結果如表11所示，在 7個系統中只發現了Uq 和 Mrh二種具活性的因子，BSSS C3，C5

16 lines
↓ Combined via 8 SC, 4 DC and 2 4-way cross
BSSS BSSSC0 BSSSC0→B14, B37
↓
169 plants testcrossed (TC) on Ia13
Cycle ↓ ↓
Co to C1 169 So Populations evaluated at locations
↓
10 S1 selected as best Performers
↓
10×10 diallel gave 45 single crosses→equal quantities of each
↓ cross contributed to bulk
seed = BSSSC1
Bulk seed random mating (RM) in rotation → = BSSSC1
C1 to C2
The BSSSS1→So→10 S1→10 × 10 diallel — bulk = BSSSC2
↘ TC on IA13
After C2 - RM eliminate RM →
etc. - etc. to BSSSC7 BSSSC5→B73
BSSSC7→B84
BSSSC7→So→10 S1→10 × 10 diallel — bulk = BS13 (S) C1 = BS13C0
BSSC0→So→10 S1→10 × 10 diallel — bulk = BSBC1
etc.

Figure 4. General diagram of the origin of the various derivatives of the Iowa Stiff Stalk Synthetic population (BSSS-) (Hallauer *et al*., 1983; Penny and Eberhart, 1971; Eberhart, Debela and Hallauer, 1973).139, 108, 84, 91, 86, and 90 plants evaluated between C1 and C6, respectively. SC, DC-single cross, double cross; TC-Test Cross; So (self) yields S1; RM-random mating; C1, C2 etc. represent the various cycles. (Peterson 1986)

對 Uq 因子來說，它們都是異質性的族群，而 BS13(S)C2 族群雖然基因組(genome)，收縮 (shrinkage)的很大，但它還是帶有 Uq，而 Mrh 在 C1, C3 族群中存在。而由 BSSS 族群選出來的自交系中，都不含任何因子，這在前述已論及可能是由於強大的人爲淘汰所致。又由另一個試驗(Cormack *et al*,1988) 利用下列方式測定 Uq 的存在與否(如圖 6)，其結果如表12所列。

由Cormack *et al*.(1988)的結果知 BSSS，Burrs white (Illinois 大學種實高低油分及高低蛋白質含量選種用的玉米族群)，Hays Golden, Iowa Long Ear, Lancaster, Kolmeier 和 BS11 的族群中都含有 Uq，這個結果更說明了 Uq 的含義 (普遍存在的 ubiquitous)，不過 Cormack 等人只測定了 Mq，其他移位因子系統是否存在尚須進一步的加以測試。

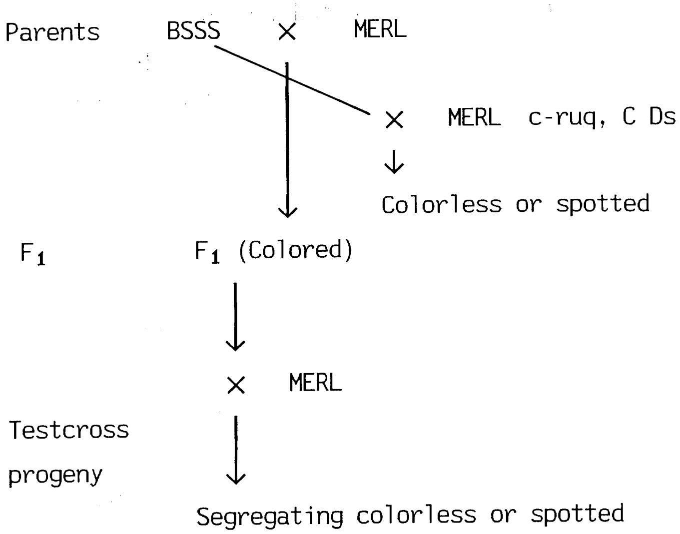
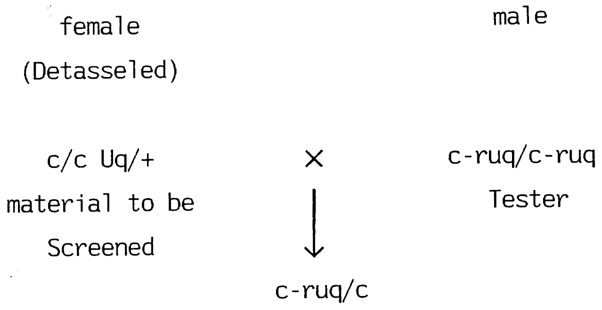


Figure 5. Crossing scheme used to uncover regulatory elements in BSSS lines in crosses to Mobile Element Receptor lines (MERL) (Peterson, 1986)

圖 6：



結　　論

1930～1970年代以美國的玉米每公頃的產量來看，它的產量還會呈直線的上升(圖 7)，而由美國 Illinois 大學玉米種實的油分及蛋白質含量的選種結果看來(圖 8)，在經過 76 個世代後正向、反向的選拔仍然繼續有效，對照前述的玉米 TE 系統的研究，及在玉米族群的分佈 (Peterson 1986, Cormack *et al*, 1988)，在玉米族群中遺傳變異的來源 TE 可能扮演了一個重要的角色。

Table 11. The distribution of active Regulatory Mobile Elements (Dt, Ac, En(Spm), Fcu, Uq, Mrh, Bg) as deduced from tests on receptor elements in source populations and derivative inbreds. Under F_2 progenies is shown the number of progenies with segregating spotted kernels over the total number of F_2 progenies. ++ = heavy mutability. Numbers refer to number of plants tested (Peterson 1986)

No. of plants tested and the distribution of F_2 progenies with elements is given for Uq and Mrh.

	Dt	Ac	En (Spm)	Fcu	Uq #	F_2 prog.	Mrh #	F_2 prog.	Bg
A. 2 to 4 gametes of BSSS series tested.									
BSSSC0	0	0	0	0	0 2		0 2		0
BSSSC1	0	0	0	0	0 2		++ 1	4/8	0
BSSSC3	0	0	0	0	++ 2	7/8, 7/11	++ 1	9/11	0
BSSSC5	0	0	0	0	++ 1	4/10	0 2		0
BSSSC7	0	0	0	0	0 1		0 2		0
BS13(S)C2	0	0	0	0	++ 2	2/12, 2/11	0 2		0
B14	0	0	0	0	0 2		0 2		0
B37	0	0	0	0	0 2		0 2		0
B84	0	0	0	0	0 2		0 2		0
B. 4-6 gametes, tested directly.									
BSSSC0	0				0 6				
BSSSC1	0				0 3				
BSSSC3	0				++ 3	1/3			
BSSSC5	0				0 3				
BSSSC7	0				0 3				
BS13(S)C2	0				++ 3	3/3			
B14	0				0 3				
B37	0				0 3				
B84	0				0 3				

C. Summary of no. of plants with elements among totals tested.

	Uq		Mrh	
	Total	With	Total	With
BSSSC1	5	0	1	1
BSSSC3	5	3	1	1
BSSSC5	4	1	2	0
BS13(S)C2	5	5	2	0

Table 12. Maize populations and inbred lines that were tested for Uq. (Cormack *et al* 1988)

MAT[a]	ID[b]	EW[c]	ET[d]	FR[e]	MAT[a]	ID[b]	EW[c]	ET[d]	FR[e]
				Populations					
BSSSCO	1	4	8		I15	3	0	1	0.78
BS13(HI)C1	1	4	13		I20	3	0	9	0.15
BS13(HI)C5	1	5	12		I25	3	1	8	
BS13(S)C1	1	3	13		I30	3	0	9	0.15
BS13(S)C4	1	10	15		JARVISCO	4	0	2	0.53
BSSS(R)C1	1	0	6	0.22	INDCHCO	4	0	2	0.53
BSSS(R)C5	1	3	14		BSLECO	5	0	9	0.15
BSS(R)C10	1	0	12	0.12	BSLE(MS)C1	5	0	12	0.12
IHOC65	2	0	11	0.13	BSLE(MS)C5	5	3	16	
IHOC75	2	0	5	0.26	BSLE(MS)C10	5	0	10	0.14
IHOC85	2	0	8	0.17	BSLE(MS)C15	5	1	4	
ILOC65	2	0	4	0.31	BSLE(MS)C20	5	0	5	0.26
ILOC75	2	0	1	0.78	BSLE(MS)C1	5	0	12	0.12
ILOC85	2	0	1	0.78	BSLE(MS)C5	5	0	12	0.12
IHPC65	2	0	6	0.22	BSLE(MS)C10	5	1	13	
IHPC75	2	0	8	0.17	BSLE(MS)C15	5	1	8	
IHPC85	2	0	3	0.39	BSLE(MS)C20	5	0	13	0.11
ILPC65	2	0	5	0.26	LC0	6	4	5	
ILPC85	2	0	2	0.53	LC1	6	0	14	0.10
RHPC21	2	3	8		LC5	6	0	13	0.11
RHPC27	2	0	2	0.53	KC0	6	2	5	
RHPC37	2	3	13		KC1	6	0	11	0.13
RLPC21	2	0	5	0.26	KC5	6	0	12	0.12
RLPC27	2	0	2	0.53	BS11C0	7	1	12	
RLPC37	2	1	4		BS11(FR)CS	7	2	11	
RHOC21	2	0	4	0.31	BS11XTE0	7	2	14	
RHOC27	2	0	17	0.08	BS16C0	8	0	17	0.08
RHOC7	2	0	11	0.13	BS16(S2)C4	8	0	15	0.09
RLOC21	2	0	6	0.22	PI213698	9	2	10	
RLOC27	2	0	5	0.26	PI213781	9	0	4	0.31
RLOC37	2	0	11	0.13	PI214195	9	0	3	0.39
SHOC14	2	1	3		PI214197	9	0	2	0.53
SHOC20	2	0	7	0.19	PI217473	9	0	6	0.22
SHOC30	2	0	8	0.17	PI217475	9	0	6	0.22
HGC15	3	0	6	0.22	PI218195	9	0	2	0.53
HGC	3	0	9	0.15	PI222470	9	1	8	
HGC25	3	2	7		PI222474	9	2	4	
HGC30	3	1	9		PI222635	9	0	3	0.39
HGOP1985	3	1	4		PI278713	9	1	5	
P10	3	0	9	0.15	PI278717	9	0	2	0.53
P15	3	0	7	0.19	PI278720	9	0	4	0.31
P20	3	0	12	0.12	PI280061	9	1	7	
P25	3	0	12	0.12	PI28053	9	1	7	
I10	3	0	1	0.78					

Tadle 12. Continued.

MAT[a]	ID[b]	EW[c]	ET[d]	FR[e]	MAT[a]	ID[b]	EW[c]	ET[d]	FR[e]
				Inbreds					
I159	10A	2	2		INDB2	10A	0	8	0.17
OS420	10A	0	10	0.14	A3G 3-1-3	10A	0	2	0.53
IND456A	10A	0	13	0.11	CI187-2	10A	0	7	0.19
IND461-3	10A	0	3	0.39	B14A	10B	0	1	0.78
ILL12E	10A	0	1	0.78	B73	10B	0	8	0.17
CI540	10A	0	4	0.31	B84	10B	0	11	0.13
ILLHY	10A	0	3	0.39	I205	11	0	2	0.53
OH3167B	10A	0	3	0.39	L289	11	0	14	0.10
LE23	10A	0	1	0.78	L317	11	0	5	0.26
TR-9-1-1-6	10A	0	9	0.15	N6G	12	0	5	0.26
FE2	10A	0	8	0.17					

a MAT = name and appropriate cycle (C20, C30, etc.)
b ID = reference.
c EW = number of ears with Uq.
d ET = total number of ears tested.
e FR = frequency that would have been detected (P=0.95) with the given number of ears (Sedcole. 1977)

ID Reference

1) Iowa Stiff Stalk Synthetic. Hallauer *et al.* (1983)
BS(HI) = half sib selection : BS13(S) = S2 selection : BSSS(R) = reciprocal recurrent selection.
2) Burr's White. Dudley (1976)
IHO = high oil selection : ILO = low oil selection : IHP = high protein selection : ILP = low protein selection : RHO = reverse high oil selection : RLO = reverse low oil selection : RHP = reverse high protein selection : RLP = reverse low protein selection : SHO = switch back high oil selection.
3) Hays Golden. Gardner (1976)
HB = Hays Golden under mass selection : I = irridaited population : P = prolific population.
4) Jarvis and Indian Chief. Moil. Bari. and Stuber (1977)
5) Iowa Long Ear. Cortez-Mendoza and Hallauer (1979)
BSLe(MS) = short ear selection : BSLE(ML) = long ear selection.
6) Kolmeier and Lancaster. Walejko and Russell (1977)
L = Lancaster : K = Kolkmeier
7) Teosinte population. Hallauer (1986. personal communication)

BS11 tested as a control for the cross between BS11 and Teosinte.

8) Eto population. Hallauer (1986. personal communication).

9) Populations from the Plant Introduction Station. Smith (1986)
PI213698 = Reid's Yellow Dent : PI213781 = Falconer : PI214195 = Longfellow : PI214197 = Minnesota 13 : PI217473 = Early Butler : PI217475 = Northern Wonder : PI218195 = Bloody Butcher : PI222470 = Pickett-Dickerson : PI222474 = Polar Dent : PI222635 = Bowman's Cole Creek : PI278713 = Eichelburger Clarage : PI278717 = Leaming : PI278729 = Woocburn : PI280061 = Lancaster Surecrop : PI280853 = Silver King.

10) Iowa Stiff Stalk Synthetic. Hallauer *et al*. (1983)
A) = inbreds that were used to develop BSSS; B) = inbreds developed from BSSS.

11) Inbred lines. Jenkins (1986)
I205 = selected from Iodent : L289 = selected from Lancaster Surecrop;
L317 = selected from Lancaster Surecrop

12) Hays Golden. Gardner (1976)
N = inbreds developed from Hays Golden.

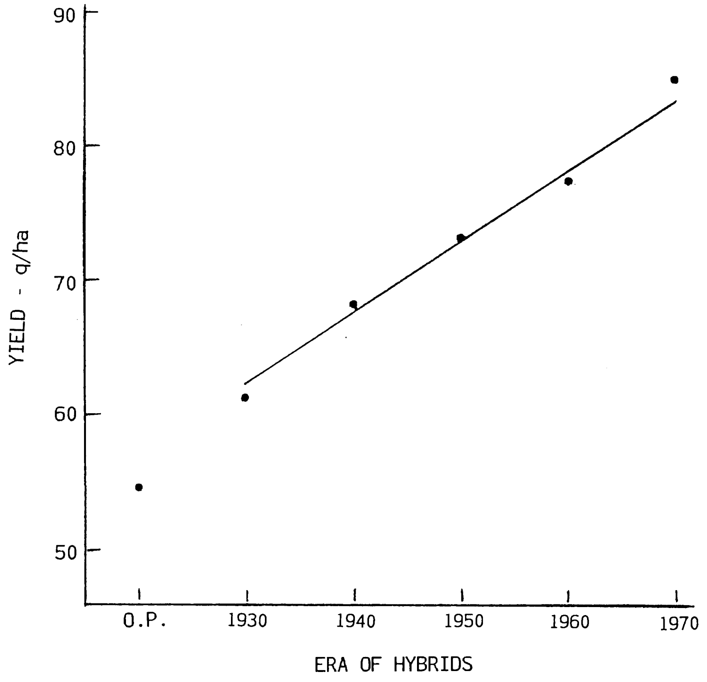


Figure 7. The predicted yields for hybrids at 10-year intervals, 1930 to 1970, based on the actual yields in Russell's study of maize hybrids representing different eras of maize breeding (after Russell, 1974). (Peterson 1986)

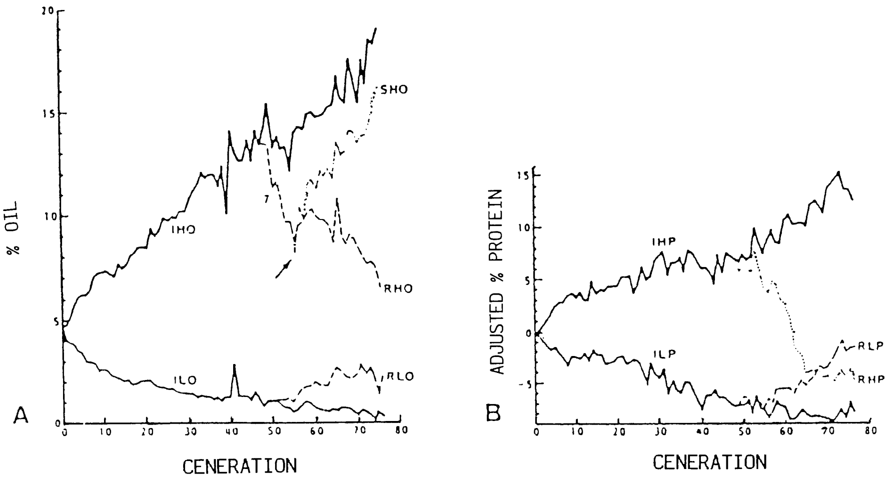


Figure 8. The manipulation of Illinois oil and protein inheritance after 76 generations of selection (Dudley, 1977). A High (IHO) and Low (ILO) Oil selection. RHO and RLO represent reverse high and low oil respectively. SHO is switchback high oil after 7 generations of RHO. (Peterson 1986)

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